

MATING BEHAVIOR AT FLORAL RESOURCES IN TWO  
SPECIES OF *PSEUDOMASARIS*  
(HYMENOPTERA: VESPIDAE: MASARINAE)

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*Abstract.*—Males of *Pseudomasaris vespoides* and *P. zonalis* (Hymenoptera: Vespidae) patrolled patches of flowers where females obtained pollen and nectar for provisioning nests. Females of each wasp species foraged only at a single plant species in the study locality, and males restricted searching to areas and times when those plants were flowering. In *P. vespoides*, both males and females spent more time in larger patches, but females spent less time in patches when males were present, probably because males harassed them. Males patrolled several patches, but frequently remained within one patch for extended periods, perching and investigating insects which entered the patch. Absolute numbers of males were low, and while interactions between males were thus rare, they were sometimes intense. No size difference could be distinguished between males that copulated and males not observed to copulate. Available data on mating behavior of *Pseudomasaris* and other masarine wasps indicates that males search for females at locations where females are concentrated in time and space, whether this occurs at nest sites, water or floral resources.

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Males are predicted to search for females at locations where receptive females are highly concentrated. In insects, if large numbers of emerging females are easily located, for example in aggregated nest sites (refs. in Thornhill and Alcock, 1983), mating may occur there. If nests are difficult to locate, or nest densities are low, males are predicted to search for females at requisite resources which are spatially and temporally restricted in availability (Emlen and Oring, 1977; Thornhill and Alcock, 1983). Patterns of male searching are expected to be influenced by both resource distribution and by female distribution at resources.

The Masarinae (Hymenoptera: Vespidae) are an unusual group of solitary wasps that closely parallel the behavior of bees in pro-

visioning their nests. Food for larvae consists of a pollen-nectar mixture, the source of which is often a limited number of plant species. North American Masarinae (*sensu* Carpenter, 1982) belong to the genus *Pseudomasaris* and are restricted to areas of moderate elevation in the western part of the continent (Richards, 1962, 1963). Despite some confusion in earlier reports concerning foraging specificity, most species probably use just one or a few host plants, particularly in a given locality (Cooper, 1952; Cooper and Bequaert, 1955).

*Pseudomasaris vespoides* specializes on flowers of *Penstemon* spp. (Scrophulariaceae), and males mate with females there (Hicks, 1929) but details of resource distribution have not been closely examined.

Similarly, males and females of *P. zonalis* have been collected at *Phacelia* spp. (Hydrophyllaceae), but little is known of specific details of behavior there. Males of solitary Hymenoptera often display one of two major behavior patterns: 1) patrolling of areas where females are present and 2) defence of areas in which females are concentrated. Males of bees that specialize on one forage plant species often defend patches of that plant (e.g. Eickwort, 1977; Alcock et al., 1981), and I predicted that where *Penstemon* or *Phacelia* was patchily distributed, males of *P. vespoidea* and *P. zonalis* would show similar behavior. Specifically, males of *Pseudomasaris* spp. are expected to concentrate mate searching at forage plants where females come for larval provisions and will defend discrete patches where females are most common. The distribution and behavior of males within and among patches should be influenced by the distribution of plants and patterns of resource use by females.

In Hymenoptera, the influence of male body size on mating success is well documented for some species (Thornhill and Alcock, 1983) and, where male-male aggressive behavior occurs, larger males often experience greater mating success.

Female *Pseudomasaris* construct mud nests, attaching them to trees and rocks (but see Dorr and Neff, 1984 for one exception to a cavity nesting female of *P. marginalis*). These nests contain several cells, up to 13 for *P. vespoidea* (Hicks, 1929) which are mass provisioned. Females scrape soil particles, which are mixed with liquid (nectar regurgitated from the crop in at least one case (Torchio, 1968)) for nest construction. Individual nests are usually dispersed and very difficult to locate (Torchio, 1968; Richards, 1963), though they may be common in some areas (Torchio, pers. comm.).

This study examines the behavior of males and females of *P. vespoidea* and *P. zonalis* at flowers with respect to male mate-locating behavior, male-male and male-female

interactions, and resource distribution and availability, and the effect of male size on mating success.

#### STUDY AREA AND METHODS

Observations were made from 22 June to 7 July 1981, 7 July to 21 July 1982, and 20 June to 18 July 1983, at Hewlett Gulch (elevation 2000 m), about 30 km northwest of Fort Collins, Colorado (Larimer Co.). A small stream flows through the gulch, which contains several open meadows.

Forage plants for *Pseudomasaris* spp. were patchily distributed throughout the gulch. The main study site for *P. vespoidea* was a large open meadow marked by many large, discrete clumps of *Penstemon unilateralis* Rydb. Thirteen major clumps and numerous isolated plants were present (Fig. 1). Clumps were categorized by number of stalks at the beginning of 1982 and 1983, and in 1983 periodic determinations of flower numbers were made.

*Pseudomasaris* activity was censused at specific clumps, and sequential checks of clumps were made several times each day to determine the presence or absence of males and females and marked individuals. In 1983, an additional large, dense clump at an isolated site further up the gulch was also studied. In addition, observations were made on each study day along a transect of several km leading to the study site. This allowed examination of other plants, sections of dirt roadway, stream crossings and other areas in the gulch for presence or absence of masarine wasps. Observations on male activity are taken from 1982 and 1983 data. Individual males were captured at flowers and marked with dots of colored enamel paint on the thorax. Head width measurements were made with Mitutoyo dial calipers. Times are given in Mountain Daylight Time.

#### RESULTS

At least three species of *Pseudomasaris* occur in Hewlett Gulch. *P. vespoidea*, one

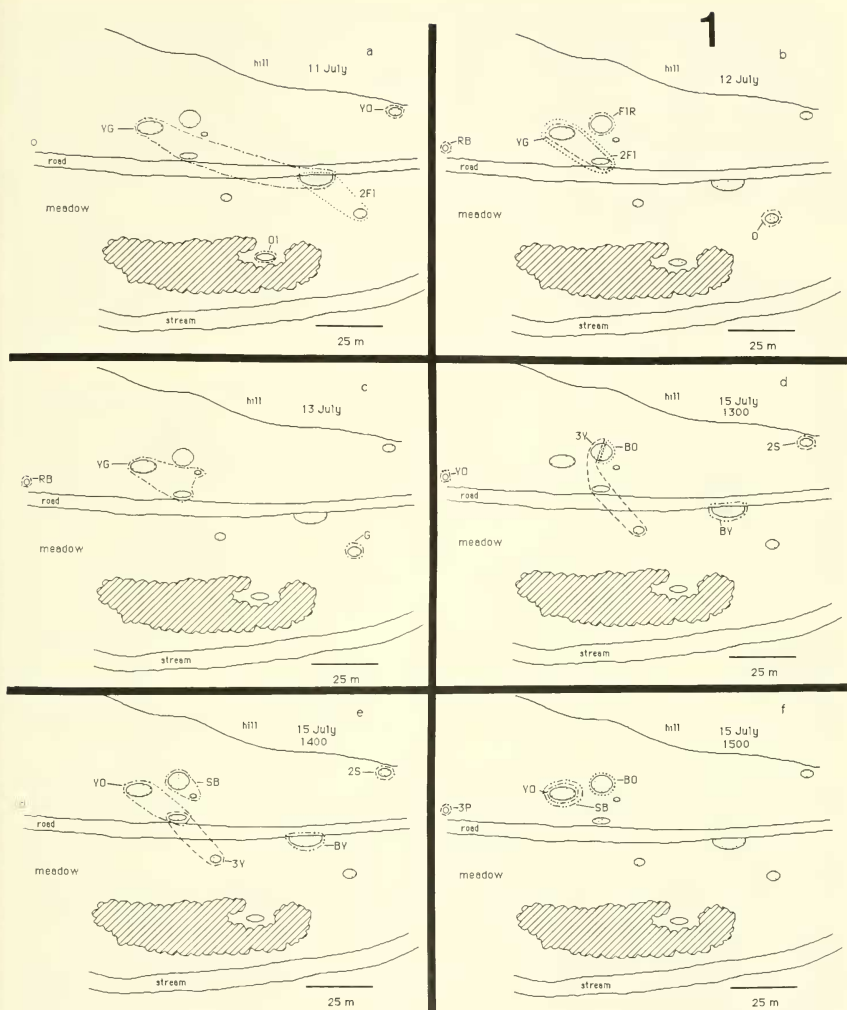


Fig. 1. Main study site indicating clumps of *Penstemon* (stippled shapes) visited by males of *Pseudomasaris vespoides* in 1983. Dotted and dashed lines enclose clumps in which males patrolled or perched. Cross-hatching shows wooded area. YG, YO, 2F1, O1, RB, F1R, O, G, 2S, BO, 3Y, BY, SB and 3P are male wasps. Maps a-d indicate changes in which clumps were patrolled or occupied over five days, d-f indicate changes in which clumps were patrolled over three hours on one day.

of the larger species in the genus, appears to be a specialist on several species of *Penstemon* (Richards, 1963), although other species may sometimes be used for forage (Tepedino, 1979). *P. zonalis* visits flowers of *Phacelia* spp. (Richards, 1963). Despite repeated searches for nests of these species, none were found, although numerous suitable nesting sites appeared to be present.

#### *Pseudomasaris vespoides*

This species was observed only at *Penstemon unilateralis*, which flowers from late June/early July to late July/early August at Hewlett Gulch. While systematic sampling of other areas was not carried out, numerous other flowering plant species were observed each day, as were stream crossings and the dirt road, but individuals of *P. vespoides* were never seen, except flying between patches of *P. unilateralis*. Plants were patchily distributed throughout the gulch, but the largest concentration was in a large open meadow. In 1983, the size of clumps of plants ranged from 2 to 158 stalks/clump in the gulch ( $\bar{x} = 61.3 \pm 52.5$ ,  $N = 19$ ), and in the main study site from 6 to 158 stalks/clump ( $\bar{x} = 61.6 \pm 56.5$ ,  $N = 14$ ). The maximum mean number of open flowers/stalk was 15.6 on 12 July.

Peak populations of *P. vespoides* occurred at different times in the three years, presumably due to differences in weather among years. In 1981, wasps were observed from 26 June to 6 July; in 1982 from 7 July to 21 July and in 1983 from 1 July to 18 July. During inclement weather (rain or cloudy or windy conditions), wasps were either absent or, under less severe conditions, males spent more time on the ground or on perches (see also Alcock, pers. obs. in Alcock et al., 1978). During rains, males occasionally sought refuge in the corolla tube of *P. unilateralis* flowers, resuming normal behavior when the sun came out (see Hicks, 1929; Cooper, 1952 for similar observations). Males and females may also spend the night in flowers (Gwynne, pers. comm.).

All clumps, and isolated single plants, were visited by males at some time. Few wasps were observed prior to 1000. Between about 1000 and 1500, when most wasps were active, the proportion of censuses during which clumps were occupied or visited by at least one male ranged from 0.5 to 1.0 in 1982 ( $\bar{x} = 0.70 \pm 0.15$ ; 138 censuses of 10 clumps) and from 0.25 to 1.0 in 1983 ( $\bar{x} = 0.63 \pm 0.20$ ; 221 censuses of 19 clumps). For females, the equivalent figures are 0.33 to 0.67 in 1982 ( $\bar{x} = 0.56 \pm 0.12$ ; 43 censuses of 6 clumps) and 0.33 to 1.0 in 1983 ( $\bar{x} = 0.66 \pm 0.31$ ; 100 censuses on 13 clumps).

Females.—Females foraged for pollen and nectar in a manner similar to that of many bees (Kevan and Baker, 1984), moving up a stalk in a spiral, entering most open flowers, occasionally visiting some blossoms more than once, and departing upon reaching the unopened immature flowers at the top of the stalk. Females foraged rapidly ( $\bar{x} = 3.4 \pm 2.7$  s/flower;  $N = 95$  flowers; 17 observations of 14 females). Numerous stalks in each clump were visited and females often visited more than one clump on a single foraging trip, before departing from the study site. The duration of female foraging visits within a clump varied widely, from 20 s to over 480 s. All but one (the exception being an unusually long visit) were from 20 s to 160 s ( $\bar{x} = 47.7 \pm 42.2$  s,  $N = 20$ ). The amount of time a female spent foraging in a clump on one visit was positively correlated with the number of flowers in the clump (Kendall's Tau:  $S = 56$ ,  $0.025 < P < 0.05$ ). Numbers of females showed a typical pattern of increase and decrease over the course of the season (Fig. 2).

Males.—In three years of study, all 60 males seen were marked and measured (11 in 1981, 21 in 1982, 28 in 1983), indicating the small numbers of males present at these sites. A large proportion of marked males was not observed after the day of marking (42% in 1981, 67% in 1982, 54% in 1983). Males present on days subsequent to mark-

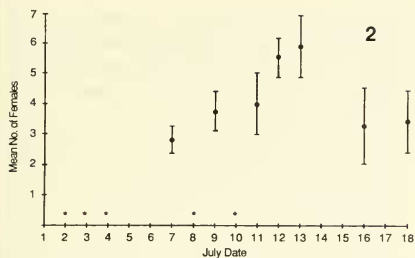


Fig. 2. Mean number ( $\pm$ SE) of females of *Pseudomasaris vespoides* (based on instantaneous samples) present in clump PH4 during 1983.

ing were present from 2 to 9 days (1981  $\bar{x}$  =  $3.7 \pm 1.7$  d; 1982  $\bar{x}$  =  $4.0 \pm 1.4$  d; 1983  $\bar{x}$  =  $4.9 \pm 2.8$  d). The maximum number of individually identifiable males (newly observed males and males previously marked) observed on different days was 8 in 1981, 12 in 1982 and 8 in 1983, although late in the season the number declined to a single male (Fig. 3). The date of the maximum number of males varied from year to year (1981—3 July; 1982—13 July; 1983—11 July).

Head capsule measurements of males were not significantly different in the three years of the study (Kruskal-Wallis test:  $\chi^2_2 = 3.32$ ,  $0.10 < P < 0.20$ ). Head capsule widths ranged from 3.55 mm to 4.0 mm ( $\bar{x}$  =  $3.81 \pm 0.11$ ,  $N = 60$ ) (Fig. 4b). One female was measured in 1983, and had a head capsule width of 4.05 mm.

Males displayed two relatively distinct mate searching behaviors, and individuals sometimes alternated between them. Males flew between numerous clumps in sequence (patrolling), perched and flew within a single clump, or both.

Males patrolled a subset of available clumps for extended periods, reiterating a particular route. Usually, clumps were rapidly examined by hovering, but occasionally, flight was interrupted by feeding at flowers, or by approaching other insects. Patrolled areas varied during the study. Males

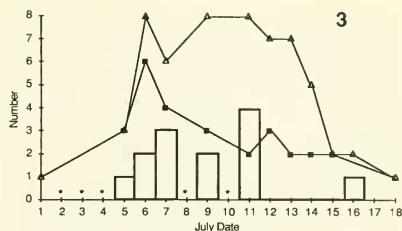


Fig. 3. Seasonal distribution in 1983 of *Pseudomasaris vespoides*. a) Total number of males observed ( $\Delta$ ); b) number of males newly marked ( $\blacksquare$ ). Frequency histogram indicates number of copulations observed. Asterisks indicate days with no observations.

usually patrolled some of the same clumps throughout a day, and occasionally on the following days as well. Patrolled areas expanded or contracted, but sometimes males shifted to an entirely different set of clumps (Fig. 1). In the three years, the number of clumps in which a given male was observed ranged from one to five over the season ( $\bar{x}$  =  $1.9 \pm 1.1$ ,  $N = 56$ ).

Patrolling flights included both large and small clumps. The mean length of visits to clumps for individual males varied from 1 s to 48 s ( $\bar{x}$  =  $4.73 \pm 7.9$  s,  $N = 79$ ), and the number of visits to a specific clump by one male during 10 min censuses varied from 2 to 10. Occasionally visits included feeding or interactions with females, thus lengthening the visitation period. For example, the duration of visits of one male ranged from 12 s to 47 s ( $\bar{x}$  =  $23.6 \pm 12.2$ ,  $N = 11$ ); if those visits involving feeding or interactions with conspecifics are excluded (i.e. only surveys for females are considered), the range narrows to 12 to 19 s ( $\bar{x}$  =  $15.3 \pm 2.7$  s,  $N = 6$ ). When only survey flights are considered, the length of time males spent examining a clump was positively correlated with the number of flowers in a clump ( $r = 0.71$ ,  $P < 0.0001$ ,  $N = 58$ ). Since males patrol numerous clumps sequentially, clump size may affect the number of clumps patrolled. The relation be-

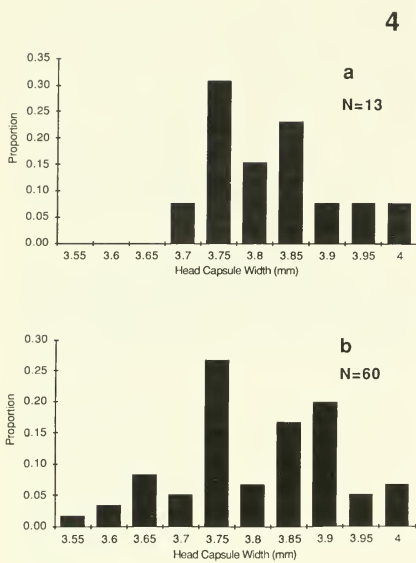


Fig. 4. Size frequency distribution of males of *Pseudomasaris vespoides* (1981–1983). Graph a, copulating males; b, all males.

tween mean time away from a clump and the number of stalks in a clump was examined, but found to be non-significant (Kendall's Tau:  $S = -9$ ,  $P < 0.10$ ,  $N = 13$ ). Similarly, number of male visits was not linearly related to mean time away from the clump.

In contrast to patrolling flights between clumps, males sometimes spent extended periods within a single clump. Males perched constantly on, or beside, a given plant for long periods of time, taking flight periodically to investigate flowers and responding to the presence of other insects, and then returning to the perch. Perch sites were usually located on the periphery of clumps, especially at small clumps or near isolated plants on patrolled routes. During observation periods, the time spent within a patch ranged from 300 s to 485 s ( $\bar{x} = 416.2 \pm 77.0$  s,  $N = 5$ ). Time males spent in the

clump under these circumstances was divided between perching and investigative flights. The percentage of time in flight varied from 8.5 to 59.6 (excluding one 6 min 16 s survey during which the male never took flight) ( $\bar{x} = 39.1 \pm 23.3$ ,  $N = 5$  surveys of 5 males for 36.6 min). For six males observed for a total of 60 min (mean observation time/male = 8 min 56 s) the mean rates of various activities were as follows: male approaches to females 0.11/min (SD = 0.11); feeding episodes 0.43/min (SD = 0.39); approaches to other insects 0.27/min (SD = 0.31). Each male foraged on one to nine flowers per feeding episode ( $\bar{x} = 4.73 \pm 2.6$ ,  $N = 57$  flowers; 12 bouts of 9 males).

The percentage of time males were recorded in clumps during censuses varied from 22.7 to 87.3% ( $\bar{x} = 53.4 \pm 28.9\%$ ,  $N = 5$  censuses of 4 males for 52.9 min total). Absences usually consisted of a series of short departures (e.g. BBY male, time away from clump  $\bar{x} = 23.9 \pm 17.5$  s,  $N = 14$ , 3Y male  $\bar{x} = 128.4 \pm 99.6$ ,  $N = 5$ ). A number of males clearly switched from perching behavior to patrolling behavior during the course of observation, and it appears that all males spend some time in both forms of mate searching. Males did not switch from patrolling to perching behavior in any observable pattern consistent among individuals. Some males patrolled at the same time as other males perched.

**Male/male interactions.**—Interactions between males usually commenced when a patrolling male passed a perched male, but also when two patrolling males met. Only 18 male/male interactions were observed in 1982 and 1983 combined, and one in 1981. As has been described for some bees (Eickwort, 1977), interactions could involve three levels of aggression: chasing, face-to-face hovering and grappling. Chasing and face-to-face hovering were sometimes characterized by one male striking another. In the course of 19 interactions, on five occasions a male oriented toward a second male and flew towards it, striking it from behind. One

male chased the other from the patch on five occasions. Swirling flights, with the two males hovering and facing each other, while moving in a circle, occurred four times, twice after an initial strike, and twice when two males observed each other at approximately the same time. At this point, males might depart the patch, with one returning. On three occasions, males contacted each other with their heads, twice while in the swirling flight. In one case, two males grappled and landed on the ground, separating immediately afterwards. One highly aggressive strike resulted in the attacked male being knocked to the ground where it remained immobile, on its back, for 3–4 s. After an interaction, one male departed the patch immediately, while the other male remained for at least a short time, before moving on to another patch, or returning to a perch. The “losing” male sometimes returned to the patch, with similar results if it was seen by the resident male.

The possible function of aggressive interactions to displace competing males can best be shown by a description of two males which concurrently occupied the upper (male marked Orange-Yellow (OY)) and lower halves (Blue-Silver (BS)) of one clump on 15 July 1982. At one point, when OY left the clump, BS began flying through the whole clump. OY returned to the upper half, and shortly thereafter, BS encroached upon the upper half of the clump. OY struck BS to the ground, the latter then flying back to the lower half, while OY flew a larger portion of the entire clump. Another confrontation occurred with a series of facing strikes, with BS retreating. This occurred a second time when OY flew further into the lower half, but BS avoided the strike and departed from the clump. Subsequently, OY patrolled much of the clump, and BS did not return.

The size of males involved in male/male interactions was known for 11 cases. Three times, the outcome was uncertain. In five cases, the larger male “won” (remained in

the clump), and three times, the smaller male won. While sample size is too small to allow statistical analysis, there is no indication that escalated confrontations (head butting, swirling flights, grappling) occur more frequently between males of roughly equal size. Males involved in swirling flights differed by at least 0.15 mm in head capsule width, and in one case by 0.35 mm. Similarly, facing strikes, as opposed to those where one male struck another from behind, occurred between males differing by the same amount. In one case where a strike knocked one male to the ground, males differed by only 0.05 mm.

Resident status of males is often difficult to determine, since two males may simultaneously patrol the same route for some time before encountering one another. Nevertheless, in 14 interactions where one male was present before a second male, the first male remained on 11 occasions. When the first male present was displaced, the second male had previously been in the patch several times, in two cases out of three.

Male/female interactions.—Interactions with females involved three levels of reaction prior to copulation. Upon sighting a female in flight or on a flower, a male usually approached her slowly, hovering behind until she settled in a flower. Sometimes a single contact (strike or touch) was all that occurred, but other times the male grasped the female from behind and began to antennate the ventral-lateral portion of the female's head capsule. The antennae of *Pseudomasaris* spp. are distinctive structures, unlike those of other vespid. The terminal segments form a club which, in *P. vespoidea*, is large and distinctly concave beneath. The placement of these clubs during copulation, possibly over the female palps, strongly implies that they play a role in copulatory behavior. A series of strokes with the antennae fully extended, moving slightly farther from the female's head with each subsequent stroke, was followed by the male extending his abdomen toward the female's genital

opening. Coupling was accompanied by violent buzzing, at which time the female often released her grip and the pair fell to the grass below, separating shortly thereafter.

During 68 observed interactions, males oriented to, but did not move toward, females on seven occasions (10%). Most frequently, a male touched or lightly struck a female (44 of 68—65%). Males grappled with females without copulating on 17 occasions (25%). Males seemed to be able to distinguish females with which they had recently attempted copulation. Males ignored a female that they had unsuccessfully mounted, even when such a female contacted the male during the course of her foraging.

Twenty-one copulations by 13 marked males were observed in the three years. In 1983 one male copulated six times, but most males were observed to copulate only once. Of a total of 71 copulation attempts observed in 1983, 58 (82%) were unsuccessful. Combining data from all years, males that copulated (i.e. the size of individual males which copulated, whether once or more than once) and size of copulating males (i.e. the size of the male for each copulation) do not differ significantly from the population size distribution ( $\chi^2$ , goodness-of-fit for males = 0.221,  $P = 0.66$ ; for copulations  $\chi^2_1 = 3.26$ ,  $P = 0.77$ ) (Fig. 4b).

Males appear to interfere with female foraging. The proportion of time females were in a clump was negatively correlated with both number of male visits, and the proportion of time males were in the clump (Kendall's Tau:  $S = -54$ ,  $P < .005$ ,  $N = 15$  and  $S = -43$ ,  $.010 < P < .025$ ,  $N = 15$ ). The mean duration of female visits was also negatively correlated with these two variables (Kendall's Tau:  $S = -37$ ,  $P < .005$ ,  $N = 11$ ;  $S = -23$ ,  $P = .05$ ,  $N = 11$ ).

#### *Pseudomasaris zonalis*

Females of *P. zonalis* foraged at clumps of *Phacelia* sp. (probably *P. hastata* Dougl. ex Lehm. Stirp.), which are typically restricted to dry, sandy patches of soil, or well-

drained hillsides in the gulch and flowered somewhat earlier than *Penstemon unilateralis*. Plant distribution varied from year to year, as did the use of plants by wasps. For example, an area with the largest concentration of plants in 1983 was never observed to be visited by wasps.

Individuals of *P. zonalis* were observed on 25 and 26 June 1981, between 16 and 28 June 1982 and between 23 June and 1 July 1983. Thirteen males were marked and measured (3 in 1981; 3 in 1982; 7 in 1983); in 1982, nine females were marked and measured. Individually marked males and females were observed returning to the same patches of *P. hastata* for up to 8 days (for individuals observed after marking,  $\bar{x} = 6.7 \pm 2.3$  d,  $N = 6$ ). Females used more than one plant/patch on a single foraging trip, and while in one case, a female interacted aggressively with other females, most encounters between females were not aggressive. Females collect soil for use in nest construction, and were observed at bare patches of soil, scraping the surface.

Males.—Males flew from clump to clump, investigating flowering plants, and they approached females from behind, attempting to copulate. Males flew a circuit of the plants in the patch, and approached different species of insects, especially leafcutting bees present on the flowers. Following a circuit, males perched on the sand and remained there, occasionally orienting to, and sometimes investigating, passing insects.

Interactions between males were rare, and usually occurred when a patrolling male passed a perched male, the latter flying up to investigate. On one occasion, a male pounced on a second male which was resting on the sand. The former immediately departed. Interactions between males and females were also infrequent. One male was observed to strike foraging females on two separate occasions, but no grapples, mounts or copulations were observed.

Some males were observed at bare patches of soil, distant from any observed host plants



but similar to sites at which females collected soil. Males perched on the sand or on plants at these sites. They made periodic short flights and occasionally departed from the site to return later. At one such site, observed over a 730 s period, a male was present for 54% of the observation period. While present, it took apparently spontaneous short flights ( $N = 28$ ), changing perches frequently. In addition, longer flights out of the immediate area occurred, involving an irregular, weaving flight following bombyliid and tachinid flies. No contact with the flies was observed.

#### DISCUSSION

The scattered distribution of nests of *Pseudomasaris* spp., combined with the concentration of females at resources required for nesting and rearing of brood, has resulted in males searching for females at sites other than nests. Some males may search at nests, or remain on their natal nests. Richards (1963) reports a male of *P. coquilletti* resting on a nest containing two unemerged females (though this may simply be a freshly-emerged male prior to departure), and sib-mating on natal nests is known from other vespids (Cowan, 1979; Jayakar and Spurway, 1966). Mating with females in or near the natal nest requires little investment in energy searching for nests. Nevertheless, searching at other sites is a major component of mating behavior in some species. If forage plants are not scarce and numbers of females at these locations are large, as is the case when females forage at only a single, or at most a few, species of plants, male searching behavior is expected to evolve to concentrate on these areas. This is the case for *P. vespoidea* and for some males of *P. zonalis* and emphasizes the convergences between these wasps and many bees (Alcock et al., 1978).

Some males of *P. zonalis* and an unidentified *Pseudomasaris* sp. in the gulch may search for females at patches of soil where

females scrape material for nest construction.

Details of the mating system of *P. vespoidea* raise a number of questions. The movement of females at *Penstemon* is probably influenced by the limited nature of pollen release and nectar secretion, which forces females to visit numerous flowers on each provisioning trip (Torchio, 1974, pers. comm.). This results in a high turnover of individuals within a given clump. Additionally, evidence suggests that not all females are receptive (or acceptable) and males which remain in one large patch will not encounter "new" females as frequently as if they move. Torchio (unpub.) has observed that females of *P. edwardsii* in the greenhouse mate more than once, but are receptive only during the periods of cell construction.

All males may spend some time patrolling a number of clumps and some time remaining within a single clump, perched and making short flights within the clump. Why do males engage in both perching and patrolling behavior? This may be an evolutionary compromise between the time and energy costs of travel between clumps, associated with patrolling, which would yield the highest encounter rate with newly foraging, virgin females, compared to less energetically expensive perching, which is coupled with a greater probability of observing and contacting all females in one area. The proportion of time spent patrolling or perching will depend on the interaction of a number of factors, possibly including air temperature, rate of female visitation at patches, and length of time within a clump of a given quality.

Perch sites appear to be located to increase observation of new females arriving at clumps. Males normally perch on the periphery of clumps. The use of perch sites beside small clumps and isolated plants may be due to these plants having a greater turnover of females, since a female cannot obtain all necessary provisions for a forage trip

from a single plant or a few plants. In these cases perching, interspersed with occasional patrolling, may provide the most energy-efficient means of encountering virgin females.

While males do not defend discrete territories, aggressive interactions occasionally occur and may serve to displace competing males from patrolling the same route. Why do males not defend a clump or several adjacent clumps, as is the case for males of some bees, such as *Hoplitis anthocopoides* (Eickwort, 1977)? Females of this species are also highly specific to forage plants used for provisioning offspring. Many of the differences between the behavior of these two species may be explained by differences in the number of males present in the area. In *H. anthocopoides*, particularly during the mid-part of the season, 60 males emerged and numerous males competed for territories around forage plants. In contrast, the largest number of males of *P. vespoidea* present in the area was 10 in 1982. This difference could explain the lack of defence since there is little requirement to spend considerable time excluding other males and the costs of patrolling territorial boundaries rather than a larger number of plants in a given area would not result in a sufficiently large increase in number of matings. Patrolling males also rarely encounter other males at any patch of plants, reducing the chance of lost time or physical damage in fights, and are likely to have access to any females encountered. Thus, there appears to be a reduced requirement to defend areas used by females against conspecific males.

The contrasting behavior of other masarine wasps indicates the importance of female distribution to male searching behavior. In contrast to examples of searching at resources, males of *P. maculifrons* perch in open areas on peaktops and ridges in central Arizona. Foraging females are scarce and widely scattered, like those of other hilltopping insects, and this probably led to the evolution of a landmark-based mating sys-

tem (Alcock, 1985). Some genera of Masarinae (*Jugurtia*, *Celonites*, *Masaris*) normally visit members of at least two families of plants (Cooper, 1952; Gess and Gess, 1980). Under such circumstances, searching for females at flowers would be much less profitable than where specific forage plant species are used. *Jugurtia confusa*, a South African masarine, nests in large aggregations of ground burrows, and males are reported flying in the nesting area and chasing females and other males, though no matings were observed (Gess and Gess, 1980). In three species of *Ceramius* (*capicola*, *linearis* and *lichtensteinii*) both females and males are present at temporary water sources. Females land on the surface of the water, presumably to collect water for nest construction, and males which patrol these water sources mount females on the water, and the pair fly off. *Ceramius* also nest in aggregations. In contrast, females of *Jugurtia* were observed at water, while males were not (Gess and Gess, 1980). These differences emphasize the importance of the distribution of females relative to emergence sites and resource availability, in the evolution of male searching behavior for mates. Further studies on the mating systems and host choice of species which appear to be polylectic, in contrast to the oligolectic North American *Pseudomasaris*, would be particularly illuminating.

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#### LITERATURE CITED

- Alcock, J. 1985. Hilltopping behavior in the wasp *Pseudomasaris maculifrons* (Fox) (Hymenoptera: Masaridae). *J. Kans. Entomol. Soc.* 58: 162-166.
- Alcock, J., G. C. Eickwort, and K. R. Eickwort. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. *Behav. Ecol. Sociobiol.* 2: 385-396.
- Alcock, J., E. M. Barrows, G. Gordh, L. J. Hubbard, L. Kirkendall, D. W. Pyle, T. L. Ponder, and F. G. Zalom. 1978. The ecology and evolution of male reproductive behavior in the bees and wasps. *Zool. J. Linn. Soc.* 64: 293-326.
- Carpenter, J. M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Syst. Entomol.* 7: 1-38.
- Cooper, K. W. 1952. Records and flower preferences of masarid wasps. II. Polytrophy or oligotrophy in *Pseudomasaris* (Hymenoptera: Vespidae). *Amer. Midl. Nat.* 48: 103-110.
- Cooper, K. W. and J. Bequaert. 1950. Records and flower preferences of masarid wasps (Hymenoptera: Vespidae). *Psyche* 57: 137-142.
- Cowan, D. P. 1979. Sibling matings in a hunting wasp: Adaptive inbreeding? *Science* 205: 1403-1405.
- Dorr, J. E. and L. J. Neff. 1983. *Pseudomasaris marginalis* nesting in logs in Colorado. *Pan-Pac. Entomol.* 58: 124-128.
- Eickwort, G. C. 1977. Male territorial behaviour in the mason bee, *Hoplitis anthocopoides* (Hymenoptera: Megachilidae). *Anim. Behav.* 25: 542-554.
- Eickwort, G. C. and H. S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. *Ann. Rev. Entomol.* 25: 421-446.
- Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 198: 215-223.
- Gess, F. W. and S. K. Gess. 1980. Ethological studies of *Jugurtia confusa* Richards, *Ceramius capicola* Brauns, *C. linearis* Klug and *C. lichensteinii* (Klug) (Hymenoptera: Masaridae) in the eastern Cape Province of South Africa. *Ann. Cape Prov. Mus. (Nat. Hist.)* 13: 64-83.
- Hicks, C. H. 1929. *Pseudomasaris edwardsii* Cr., another pollen provisioning wasp, with further notes on *P. vespoides*. *Can. Entomol.* 61: 121-125.
- Jayakar, S. D. and H. Spurway. 1966. Re-use of cells and brother-sister mating in the Indian species *Stenodynerus miniatus* (Saussure) (Vespidae: Eumeninae). *J. Bombay Nat. Hist. Soc.* 63: 368-378.
- Kevan, P. G. and H. G. Baker. 1984. Insects on flowers, pp. 607-631. In Huffaker, C. B. and R. L. Rabb, eds., *Ecological Entomology*. Wiley and Sons, Ltd., New York.
- Richards, O. W. 1962. A revisional study of the masarid wasps (Hymenoptera: Vespidae), British Museum (Natural History). William Clowes and Sons, Ltd., London. vii + 294 pp.
- . 1963. The species of *Pseudomasaris* Ashmead (Hymenoptera: Masaridae). *Univ. Calif. Publ. Entomol.* 27: 283-310.
- Tepedino, V. J. 1979. Notes on the flower-visiting habits of *Pseudomasaris vespoides* (Hymenoptera: Masaridae). *Southwest. Nat.* 24: 380-381.
- Thornhill, R. and J. Alcock. 1983. The evolution of insect mating systems. Harvard Univ. Press, Cambridge, Mass. ix + 547 pp.
- Torchio, P. F. 1970. The ethology of the wasp, *Pseudomasaris edwardsii* (Cresson), and a description of its immature forms (Hymenoptera: Vespoidea: Masaridae). *L.A. Co. Mus. Contrib. in Sci.* 202: 32 pp.
- . 1974. Mechanisms involved in the pollination of *Penstemon* visited by the masarid wasp, *Pseudomasaris vespoides* Cresson. *Pan-Pac. Entomol.* 50: 226-234.